CHROMOSOMES OF THE BOWHEAD WHALE

(*BALAENA MYSTICETUS* LINNAEUS)

A

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CHROMOSOMES OF THE BOWHEAD WHALE

(BALAENUS MYSTICETUS LINNAEUS)

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ABSTRACT

The somatic chromosomes of the bowhead whale, Balaena mysticetus, are described for the first time using homogeneous staining and trypsin G-banding. The diploid chromosome number in all cells studied is 42. The bowhead karyotype retains many features of the general 2n = 44 cetacean karyotype from which it is derived, yet it is the first mysticete for which a chromosome number other than 2n = 44 has been reported. The advanced karyotype of the bowhead may reflect greater anatomical specialization of this whale than of other mysticetes. Cytogenetic data for cetaceans are reviewed within the framework of a model of speciation in sympatry.

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TABLE OF CONTENTS

INTRODUCTION

The considerable evolutionary radiation of the whales, dolphins, and porpoises contrasts sharply with their extremely conservative rate of karyotypic change. The Cetacea are so morphologically divergent that the common ancestry of the toothed whales and baleen whales has been the subject of ongoing controversy (Gaskin, 1976). In spite of a diverse array of ancient taxa, a recognizably similar karyotype is shared by most living cetaceans. Arnason (1974b) reasoned that their great mobility, combined with a slow reproductive rate, may explain the conservative chromosomal evolution of the whales and of the pinnipeds. Arnason (1969) proposed a monophyletic origin for odontocetes and mysticetes, based on the profound chromosomal similarity of the two groups; this is now supported by evidence involving homologous satellite DNAs (Arnason, pers. comm.) and chromosome banding from many species of each suborder (Duffield, 1977). The fossil record indicates that the latest period in which the odontocetes and mysticetes could have diverged is the late Eocene (Simpson, 1945). The basic cetacean karyotype has been conserved from at least that time.

Although the role of chromosomal change in evolution is not well understood, several papers by Wilson and

colleagues (Bush et al., 1977; Maxson and Wilson, 1975; Prager and Wilson, 1975; Wilson, 1976; Wilson et al., 1974a, 1974b, 1975) have compared rates of evolution at the chromosomal, genic, and morphological levels. They have concluded that rapid chromosomal evolution facilitates rapid speciation and morphological evolution. Evidence that chromosomal change results in alteration of genetic regulation was presented by Wilson (1976). These authors (Bush et al., 1977; Wilson et al., 1975) have argued that the social behavior of many mammals produces small effective population sizes which last for several generations. Inbreeding can then promote rapid fixation of chromosomal mutations. Chromosomal evolution seems fastest in genera with clans and harems (e.g., some primates and horses) or with limited vagility and dispersal (e.g., some rodents).

Cytogenetic study of the bowhead or Greenland right whale, Balaena mysticetus, has been undertaken in an effort to examine its relationships to other species of whales and to expand our understanding of cetacean evolution. A form of bowhead called "ingutuk" by Inupiat Eskimos is distinguished by several morphological features. It is hoped that continued cytogenetic investigation will eventually permit the evaluation of intraspecific variation in this species.

METHODS

During May 1977 I collected tissues from one male and three female bowheads during the Eskimo hunt at Barrow, Alaska. None of the whales sampled was an ingutuk. Approximately 50-gram pieces of skin, lung, or kidney (two of the three from each animal) were taken a few hours post-mortem in the course of helping butcher the animals. The tissue was carried in plastic bags and protected from freezing by keeping it under heavy clothing near the body of the courier. In one case viable tissue was flown directly to Fairbanks in this manner and cultures were initiated within 48 hours. Usually it was possible to aseptically explant small pieces (about 5-mm cubes) of tissue into tissue culture medium. Thus preserved, the tissue was stored at 10° C until transported to Fairbanks where culturing was initiated.

Cultures were established and maintained by the conventional methods of mammalian tissue culture (Rausch and Ritter, 1973). Cell lines were split 1:2 at most passages and duplicate flasks were harvested for karyotyping when about 80% confluent. After sufficient material had been harvested from each whale the cell lines were stored in liquid nitrogen for possible later use. Most of the material was in storage before the fifth passage. These

cell lines are being shared with Dr. Ulfur Arnason at the University of Lund in his study of cetacean satellite DNAs.

Colcemid (0.6 µg/ml) was added to incubating cells 1.5 hours prior to harvesting. Harvested cells were treated with 0.075 M KCl hypotonic solution for about 8 minutes and fixed in freshly prepared Carnoy's fixative. Air dried preparations were stained with carbol-fuchsin or 2% Giemsa in phosphate buffer. Trypsin G-bands were induced by the method of Wang and Federoff (1972).

RESULTS

Chromosomal counts from at least ten cells of each tissue revealed a diploid number of 42 for all individuals and tissues. The homogeneously stained male karyotype is shown in Fig. 1. The chromosomes are arranged in four groups according to their arm ratios (r) as suggested by Levan et al. (1964). Chromosomal measurements were performed on five cells from the male. The absolute length of the female haploid set averaged 96μ. The results of the chromosomal measurements are given in Table 1. Due to their minute size, the short arms of the telocentric chromosomes were not measured separately but were included in the total length of the chromosomes. The metacentric (m) group (r = 1.00-1.67) is composed of nine pairs; the submetacentric (sm) group (r = 1.67-3.00) five pairs; the subtelocentric (st) group (r = 3.00-7.00) three pairs; and the telocentric (t) group (r > 7.00) three pairs. The X is a metacentric chromosome, as is the small Y. The subtelocentric and telocentric groups are easily recognized in conventionally stained karyotypes, whereas some of the metacentric and submetacentric group chromosomes are less distinct. The m1 and sm1 chromosomes are conspicuously the largest within their respective groups. The m7 pair is characterized by a secondary constriction in the short arms. The frequent

attachment of these homologues to each other indicates the presence of a nucleolus organizer. A similar finding has been described in other cetacean species (Arnason, 1974a). In the 23 cetacean species examined by Duffield (1977), chromosomes showing attachment were regarded as acrocentric. Irrespective of the different groupings by Arnason and Duffield, it appears that a pair with the same characteristics is being described. In the bowhead, however, the short arms seem to be somewhat larger than in other cetacean materials. This was particularly prominent in one of the female specimens which showed a striking heteromorphism in the size of the satellite knobs between the two homologues.

G-banding of cells from the male and one female enabled positive identification of the whole complement. A G-banded karyotype of the bowhead is shown in Fig. 2. Many of the more distinctive bowhead chromosomes have G-banded patterns similar to their counterparts in the balaenopterid karyotypes presented by Arnason (1974a) and Arnason et al. (1977). The X is the second largest metacentric chromosome. It makes up 5% of the female haploid set and is thus of the "original" type (Ohno et al., 1964). The G-band pattern of the X coincides with the pattern shown in other cetaceans (Arnason, 1974a; Arnason et al., 1977; Duffield, 1977).

TABLE 1. Chromosome measurements of Balaena mysticetus.

Chromosome	Relative length* mean	SE	Absolute length** mean	limits	Arm ratio mean	SE
m1	7.92	0.734	7.61	5.64-11.67	1.35	0.174
m2	4.75	0.310	4.51	3.44-6.01	1.38	0.138
m3	4.07	0.377	3.84	2.74-4.56	1.38	0.234
m4	3.61	0.247	3.43	2.41-4.17	1.52	0.163
m5	3.45	0.233	3.30	2.35-4.87	1.34	0.282
m6	3.14	0.183	2.99	2.04-3.92	1.16	0.127
m7	2.95	0.585	2.78	1.75-3.40	1.17	0.168
m8	2.83	0.218	2.71	1.67-3.46	1.34	0.138
m9	2.74	0.214	2.63	1.62-3.29	1.15	0.100
sm1	7.31	0.404	7.05	5.00-9.14	1.98	0.140
sm2	5.58	0.543	5.33	3.84-6.49	1.99	0.179
sm3	4.66	0.457	4.48	2.50-6.10	1.96	0.246
sm4	4.39	0.187	4.21	2.94-5.28	2.18	0.146
sm5	3.55	0.163	3.40	2.32-4.69	1.83	0.147
st1	7.78	0.510	7.48	5.22-10.96	4.68	0.723
st2	7.55	0.602	7.26	5.04-10.92	3.74	0.496
st3	6.01	0.374	5.44	4.43-7.54	3.82	0.402
t1	4.83	0.446	4.67	3.18-7.02	>7.00	____
t2	4.45	0.322	4.29	3.07-6.40	>7.00	____
t3	3.44	0.241	3.33	2.13-4.69	>7.00	____
X	4.96	0.188	4.59	3.40-6.47	1.52	0.110
Y	0.71	0.467	0.87	0.33-1.42	____	____

* Percent of female haploid length (A+X)
** Microns

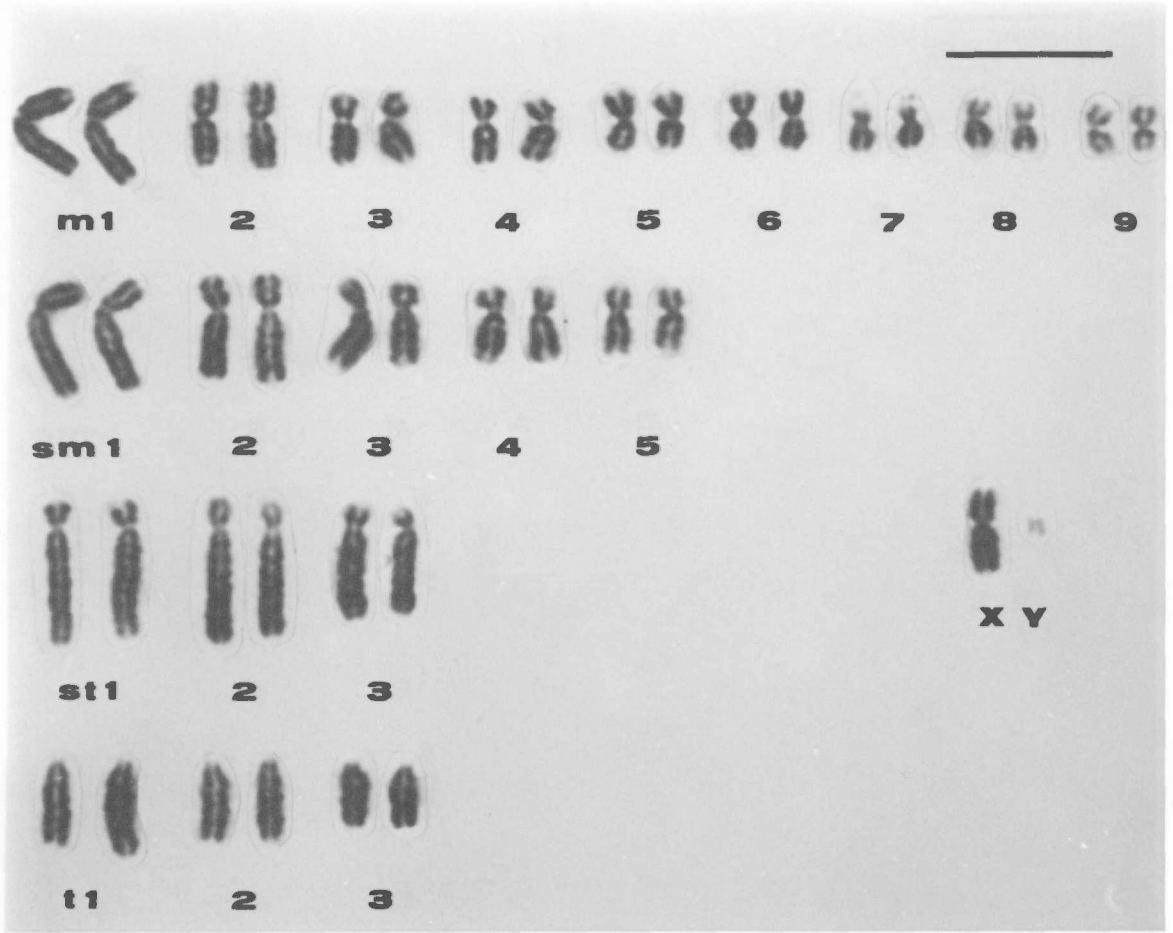

Fig. 1. Karyotype of male Balaena mysticetus, 2n = 42. The bar is 10 microns.

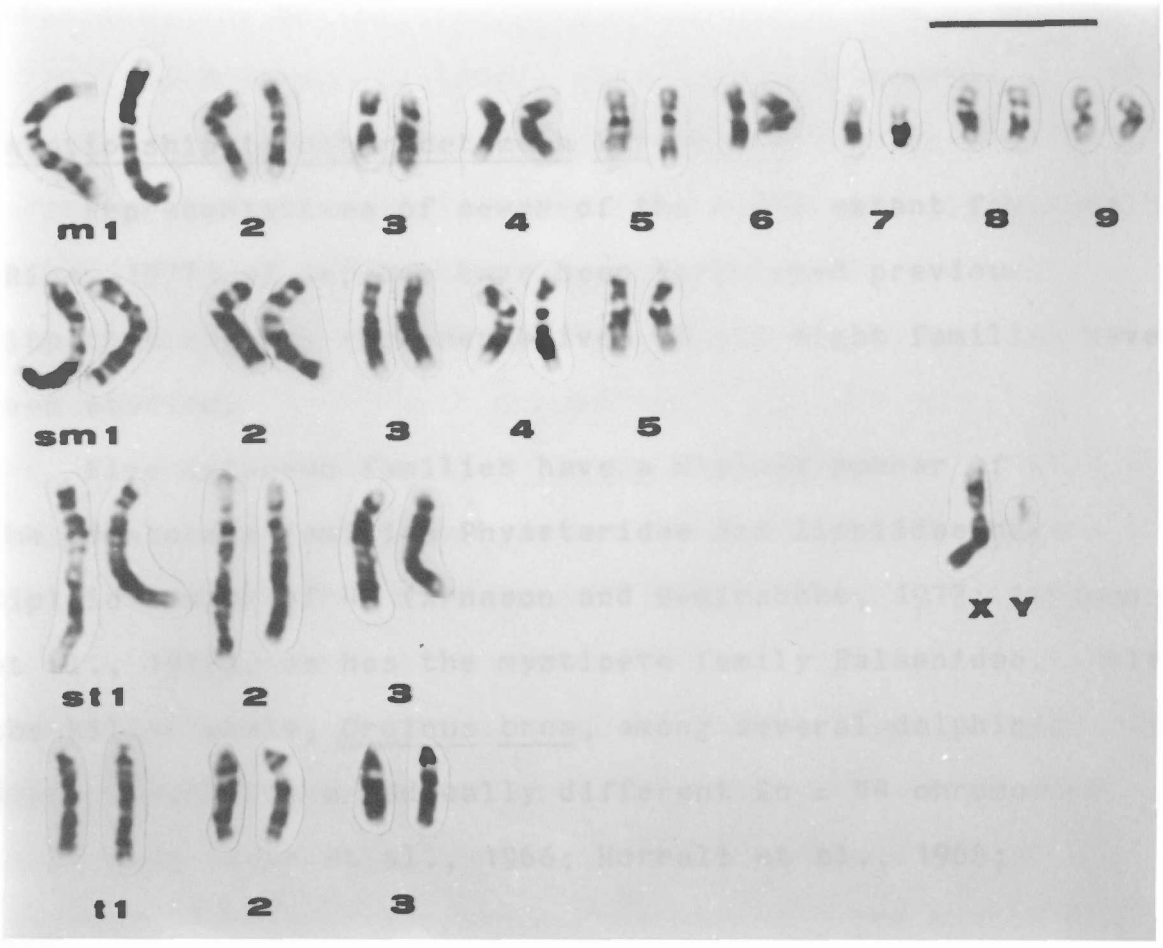

Fig. 2. G-banded karyotype of Balaena mysticetus. The bar is 10 microns.

DISCUSSION

Relationship to other cetacean karyotypes

Representatives of seven of the eight extant families (Rice, 1977) of Cetacea have been karyotyped previously. With this report, representatives of all eight families have been studied.

Five cetacean families have a diploid number of 44. The odontocete families Physeteridae and Ziphiidae have a diploid number of 42 (Arnason and Benirschke, 1973; Arnason et al., 1977), as has the mysticete family Balaenidae. Only the killer whale, Orcinus orca, among several delphinids studied exhibits a radically different 2n = 44 chromosome morphology (Carr et al., 1966; Horrall et al., 1968; Duffield, 1977).

Duffield (1977) suggests that the harem-forming social structure of Orcinus and Physeter predisposes them to rapid chromosomal evolution. In such a social structure, relatively few individuals contribute gametes to successive generations and small discrete breeding units are defended. This results in a small effective population size, which appears to be necessary for the fixation of chromosomal mutations. Thus, the sperm and killer whales seem to be subject to more rapid chromosomal evolution than other

cetaceans, due to the causes suggested by Wilson et al. (1975) and Bush et al. (1977) for mammals in general.

The same explanation could be postulated for the karyotypes of the beaked whales (Ziphiidae) and pigmy sperm whales (Kogia), which, with Physeter, comprise the Physeteroidea. Their social organization is unknown but the sexual dimorphism of both groups could well be correlated with polygamy as it is in Physeter and Orcinus.

The bowhead karyotype is easily related to the "general mysticete karyotype" of Arnason (1974a). The four mysticete species he examined, like most odontocetes, have a diploid number of 44, and the homologues of the smallest pair in the complement frequently show attachment by their short arms; there are four pairs of telocentric chromosomes and three large pairs of subtelocentric chromosomes. The number of metacentric and submetacentric chromosomes varies slightly among the four species studied by Arnason. All of the metacentric chromosomes are relatively small.

The bowhead differs from the typical mysticete in two important respects: the reduction in number from 2n = 44 to 2n = 42 is due to the absence of one of the four pairs of telocentric chromosomes, and the largest pair of metacentric chromosomes is unique. The largest metacentric chromosomes in conservative 2n = 44 cetaceans have a length of about 5% of the female haploid set. In the bowhead the

m1 chromosomes are 8% of the female haploid set. This configuration suggests that the large bowhead m1 may be the result of fusion of the "absent" telocentrics with another pair. Although it is independently derived, the 2n = 42 karyotype of Mesoplodon (Ziphiidae) also involves the absence of a fourth pair of telocentric chromosomes (Arnason et al., 1977).

Fusion of chromosomes and reduction in diploid number tend in certain mammalian groups to correlate with evolutionary advancement (Matthey, 1973). The fact that many features of the "general mysticete karyotype" are shared with odontocetes shows that the 2n = 44 general cetacean karyotype is ancestral to other karyotype forms. The bowhead karyotype is therefore derived and advanced relative to other mysticete karyotypes.

Two factors may relate to this condition:

1) Of the three extant families of mysticetes, balaenids are the oldest in the fossil record (Simpson, 1945). From this it could be argued that they have had the most time to diverge from the cetothere ancestors of the living mysticetes. The extreme elongation of the balaenid skull and complete fusion of the cervical vertebrae are advanced conditions that coincide with the relative age of the group. The bowhead is the most advanced balaenid with regard to skull elongation.

2) The polar pack ice which bowheads inhabit may have provided an excellent isolating mechanism for small groups of animals in which a chromosomal fusion could become fixed. The bowhead's environment appears more structured than that of other mysticete whales. It will be interesting to see whether the confamilial black right whale, Balaena glacialis, and the pigmy right whale, Caperea marginata, share the 2n = 42 karyotype.

Thus, while the bowhead retains most features of the general cetacean karyotype, it is not yet possible to know whether the major distinction is a product of the long balaenid lineage or the isolating effect of the bowhead's pagophilic habits.

Cetacean speciation

The mechanism whereby speciation has occurred on a wide scale with little chromosomal change is almost certainly related to the panmictic nature of cetacean populations. However, two opposing interpretations, allopatric versus sympatric speciation, can be argued.

Arnason (1972 and 1974b) interpreted the karyotypic uniformity within the cetaceans and pinnipeds as showing that allopatric speciation prevails in these groups. He contrasted these marine mammals to the rodents and insectivores which, because of their high fecundity, low vagility, and comparatively structured environment, have a

stronger tendency to inbreed. In such populations, animals with identically rearranged karyotypes have a relatively high probability of founding new karyotypic populations. Rodents and insectivores show considerable karyotypic diversity, and speciation is considered by Arnason to be of White's (1968) stasipatric mode.

Although the variability of karyotypes between cetacean taxa is extremely low, intraspecific variability is pronounced in carefully studied species. This heteromorphism is demonstrated by C-bands, which are predominantly noncentromeric, in contrast to those of other mammals. The bands make up about 25% of the total length of mysticete chromosomes that have been studied (Arnason, 1974a).

The genetic effect of heterochromatic segments is not yet clear and the phenomenon of high intraspecific chromosomal variability in a taxon with low interspecific variability is enigmatic. Recent studies (summarized by Jones, 1977) indicate that one effect of heterochromatic segments is the inhibition of chiasma formation. The differential accumulation of heterochromatin exhibited by C-band heteromorphism can be assumed to cause some degree of euchromatin-heterochromatin overlapping between chromosomes in meiosis (Arnason et al. 1978). The effect of large localized segments of heterochromatin would be to

isolate substantial portions of the surrounding euchromatin from chiasma formation. The genes on such an asynaptic segment, isolated from recombination, would be free to evolve independently as supergenes while the nontranscribed heterochromatin would be conserved. The phenotypic expression of such a mechanism would presumably be intraspecific polymorphisms.

Recent work by Arnason (pers. comm.) shows that much of the heterochromatin in cetacean karyotypes consists of satellite DNA that has been conserved in both odontocetes and mysticetes. Another satellite is conserved in three balaenopterid whales. Both satellite DNAs are located in C-bands (Arnason et al., 1978). The conservation of these satellite DNAs at routinely heteromorphic sites suggests that heterochromatin-induced polymorphisms have been important in cetacean speciation.

The natural history of cetaceans suggests that diversification by intrapopulational polymorphism is an alternative to allopatric speciation proposed by Arnason (1972 and 1974b). Arnason weighed the data in terms of an allopatric-stasipatric dichotomy for speciation. Other modes of speciation were not considered.

The panmictic nature of cetacean populations should tend to inhibit evolution by chromosomal mutation as explained by Arnason. In invoking the allopatric mode of

speciation he assumed that divergence occurred between geographically isolated populations, each of which was panmictic within itself, and hence this divergence involved little karyotypic change. Within the presently recognized modes of mammalian speciation, this is the parsimonious interpretation of the cytogenetic data from cetaceans and pinnipeds.

White (1978) recently observed that, "Speciation mechanisms in marine organisms are, in general, poorly understood. Species of such wide-ranging fish as tunas would seem to be forms in which allopatric speciation due to complete geographic isolation could not be expected." Certainly cetaceans also are sufficiently wide-ranging to stretch the credibility of speciation in allopatry. Not only are they the most mobile of mammals, but their long generation time would require geographic isolating mechanisms of exceptional duration in the relatively uniform marine environment. Nor is evolution by allopatric speciation supported by the anti-tropical distribution of most mysticete species.

Given that these are sufficient grounds for questioning the applicability of the allopatric model of speciation, and that we can dismiss White's (1968) stasipatric model for the reasons proposed by Arnason, we are left with the controversial sympatric models of speciation. Although

White (1978) clearly accepts the possibility of sympatric speciation, he points out the "rather woeful lack of evidence as to the exact nature of the genetic processes involved."

The evidence of sympatric speciation most relevant to the problem considered here seems to be from laboratory work on disruptive selection (i.e., selection favoring extreme at the expense of average phenotypes). Thoday and Boam (1959) produced simultaneous divergence for a polygenic character and ethological isolation in Drosophila melanogaster by disruptive isolation for chaeta number. Subsequent workers have not been able to reproduce this experiment (White, 1978). However their work stimulated a mathematical analysis by Maynard Smith (1966) from which he concluded that, "the crucial step in sympatric speciation is the establishment of a stable polymorphism in a heterogeneous environment. Whether this paper is regarded as an argument for or against sympatric speciation will depend on how likely such a polymorphism is thought to be, and this in turn depends on whether a single gene difference can produce selective coefficients large enough to satisfy the necessary conditions...."

There are two points that make these conclusions particularly relevant to whales:

1) Maynard Smith demonstrates that "if the population inhabits two subenvironments or 'niches,' the population size being separately regulated to numbers N_1 and N_2 in the two niches, and if AA is fitter in one niche and aa in the other, then a stable polymorphism is possible, even if there is random mating between individuals raised in the two niches." I would further argue that not only is it "possible," but such a situation would produce selective pressure for polymorphism. This is the only way in which a panmictic population could specialize to exploit alternative niches. These circumstances would seem to have a high probability of arising in migratory organisms which may do a major part of their feeding in a heterogeneous environment but mate in a separate area where mate selection is not influenced by the heterogeneity of the feeding environment. No matter how much their feeding habitat may diversify, either spatially or temporally, such organisms remain genetically panmictic on their breeding ground. Isolation of unassorted segments of the genome would allow specialization to exploit the diverse feeding habitat. Such selective pressure for polymorphism could amplify the amount of C-heterochromatin if this material does, in fact, cause polymorphism. Selection for the increase of C-heterochromatin might explain the large amounts of this material in cetacean karyotypes. This is consistent with

the interpretation of Greenbaum and Baker (1978) that noncentromeric heterochromatin in Peromyscus (Rodentia) is derived rather than primitive and may therefore improve fitness.

2) If Maynard Smith's "single gene difference" were a "supergene" caused by a chromosomal rearrangement or heterochromatin-induced polymorphism, as proposed by Arnason et al. (1978), it could well "produce selective coefficients large enough to satisfy the necessary conditions...."

Having mathematically established the proposition that in a heterogeneous environment a stable polymorphism can be maintained by disruptive selection, Maynard Smith proposed four conditions under which reproductive isolation might evolve between the morphs. The first is "habitat selection," by which individuals have a tendency to return for mating to the habitat in which they developed. This could be regarded as allopatric speciation in which isolation is behavioral rather than geographic. This condition would not apply to migratory organisms for which I have proposed the opposite condition as a cause of polymorphism. However allochronicity of the two niches might have the same effect (i.e., assortative mating), and temporal heterogeneity may be of particular importance in the marine environment. The second condition is "plieotropism" in which the niche-adapting genes themselves

cause assortative mating. Maynard Smith regarded this as unlikely but White (1978) pointed out that, "it may be slightly more plausible in the case of chromosomal rearrangements affecting whole blocks of genes." The third way is by the occurence of "modifier genes" which modify the effect of the initial polymorphism to produce assortative mating. The fourth condition is isolation by separate "assortative mating genes" which, if there is "some degree of habitat selection by egg-laying females," could evolve linkage to the niche-adapting genes. The "habitat selection" would apply equally well to female mammals rearing their offspring in the habitat in which they were raised.

The scarcity of clear geographic barriers and the extreme mobility of whales is not suggestive of allopatric distribution. Given a possible chromosomal mechanism for the genetic divergence of these organisms it is tempting to speculate that the evolutionary radiation of cetaceans could well have involved a process of selecting from distinct morphs occuring within large, freely-interbreeding populations. In this case, the isolating mechanism permitting original divergence may have been intergenomic rather than interorganismic. These intergenomic isolating mechanisms may be cytologically visible as C- or G-band heteromorphisms. Examining these features in a species of

whale which appears to be polymorphic would test the potential of this sympatric model of cetacean speciation. The bowhead shows more promise than other whales of being such a species.

The Inupiat Eskimos have long recognized a form of the bowhead called the "ingutuk." Bailey and Hendee (1926) and Stephanson (1944) noted and described this type of whale but a better description of the ingutuk is in an unpublished manuscript by the anthropologist D.C. Foote (1964). Although they certainly seem to be bowheads, ingutuks have shorter baleen, a flatter head, a greater girth, and denser bones than regular bowheads. Some Eskimo informants insist that all ingutuks are females, although four whales designated as ingutuks and fitting the description have been males (Foote, 1964 and personal observations in 1978 and 1979). However the possibility exists that the sex ratio of this morph is skewed. Since the ingutuk is described by a suite of characters, the characters must have co-evolved in some way. That so specialized and important an organ as the baleen differs in these whales is further suggestive of significant divergence.

The apparently discontinuous variation presented by the ingutuk could be due to intraspecific polymorphism, some degree of reproductive isolation, or discontinuously expressed phenotypic variation caused by some environmental factor.

The question of cetacean speciation in sympatry, versus allopatry, requires further study of the functional aspects of constituitive heterochromatin as well as more precise studies of intraspecific chromosomal variability in whales.

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